Postprint: Reproductive and Stress-Tolerance Traits of Wild Oat and Its Allelopathic Effects on Wheat

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Abstract

As a widely distributed malignant weed in farmland, wild oat exhibits strong adaptability to environmental stress and often occupies a dominant position in interspecific competition. This study investigated the reproductive and dispersal characteristics of wild oat populations, the stress resistance traits of its seeds and seedlings, and the allelopathic effects of its root exudates on wheat, aiming to provide references for developing effective control measures. The results showed: (1) Wild oat possesses strong seed reproduction and dispersal capabilities, flowering and fruiting earlier than wheat, with high seed yield, substantial underground seed reserves, and long dispersal distances; (2) Wild oat seeds have a broad temperature adaptation range, germinating normally under both constant and variable temperature conditions, with freezing followed by room temperature being the optimal germination condition, achieving a total germination rate of 93.33%; (3) Wild oat seeds demonstrate certain adaptability to salt stress, capable of normal germination in NaCl solutions at concentrations below 1.8%; (4) Wild oat seedlings show strong adaptability to both salt and drought stress; as NaCl and PEG concentrations increased, the proline content in wild oat seedling leaves increased significantly ($P<0.01$), while catalase activity exhibited a trend of initial increase followed by decrease; (5) The aqueous root extract of wild oat had extremely significant effects on wheat seedling plant height, dry weight, root length, and root vitality ($P<0.01$), proving that wild oat root exudates have allelopathic effects on wheat seedling growth. These results indicate that the competitive advantages of wild oat are primarily manifested in its strong reproductive and dispersal capabilities, robust stress resistance, and allelopathic effects, and related research can provide theoretical references for large-scale wild oat control.

Full Text

Preamble

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Reproductive and Stress Resistance Characteristics of Wild Oat and Its Allelopathic Effects on Common Wheat

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Abstract: As a widespread malignant weed in farmlands, wild oat possesses strong adaptive capacity to environmental stresses and often occupies a dominant position in interspecific competition. This study investigated the reproductive and dispersal characteristics, stress resistance of seeds and seedlings, and the allelopathic effects of root exudates on common wheat, aiming to provide references for developing effective control measures. The results showed: (1) Wild oat exhibits strong seed reproduction and dispersal capacity, with earlier flowering and seed setting than wheat, high seed yield, large underground seed reserves, and long dispersal distances; (2) Wild oat seeds adapt to a wide temperature range, germinating normally under both constant and variable temperatures, with freezing followed by room temperature being the optimal condition for germination, achieving a total germination rate of 93.33%; (3) Wild oat seeds demonstrate certain adaptability to salt stress, germinating normally in NaCl solutions below 1.8% concentration; (4) Wild oat seedlings show strong adaptability to both salt and drought stress, with proline content in seedling leaves increasing significantly ($P<0.01$) as NaCl and PEG concentrations increase, while catalase activity shows an initial increase followed by a decline; (5) Wild oat root aqueous extract has highly significant effects ($P<0.01$) on wheat seedling height, dry weight, root length, and root vitality, confirming the allelopathic effect of wild oat root exudates on wheat seedling growth. These results indicate that the competitive advantages of wild oat are manifested through robust reproductive and dispersal capacity, strong stress resistance, and significant allelopathic effects. Related research can provide a theoretical basis for wild oat control in farmlands.

Keywords: Wild oat; Reproductive characteristics; Stress resistance; Allelopathic effect; Competitive advantage

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Introduction

Wild oat (*Avena fatua* L.) is an annual or biennial herbaceous plant in the Poaceae family and a malignant farmland weed distributed across Europe, North America, Africa, Australia, and temperate-cold regions of Asia. With strong tillering ability, high reproductive rates, and broad adaptability, it poses a major threat to field crops. Currently, approximately 1.6 million hectares of farmland across 16 provinces in China are infested with wild oat, with damage rates reaching 15.6% in winter wheat regions and 25.3% in spring wheat regions, causing annual grain losses of about 1.75 billion kilograms.

Wild oat plants resemble wheat (*Triticum aestivum* L.) in appearance but grow more rapidly. Their well-developed root systems compete directly with wheat for soil moisture and nutrients, while their extensive soil seed banks maintain strong reproductive capacity and enable them to survive adverse environmental conditions and avoid predation through seed dormancy. Wild oat also exhibits strong tolerance to certain environmental stress factors, growing well under heavy metal pollution and phenolic acid stress conditions. These growth, reproductive, and stress resistance characteristics often place wild oat in a competitive advantage over wheat.

Effective wild oat control faces numerous challenges. Conventional methods include seed selection before wheat sowing, manual removal, field rotation, and chemical herbicides. However, seed selection and manual removal are costly and ineffective, while field rotation is constrained by geographic location and farming practices. Consequently, chemical herbicide application has become the primary control measure, despite several drawbacks: (1) early application shows obvious effects but efficacy declines later, and mixing multiple herbicides increases costs; (2) herbicides only kill aboveground plants without eliminating underground reproductive organs; (3) potential risks exist for reducing wheat food safety and polluting the environment; and (4) long-term use gradually leads to herbicide resistance in wild oat. Therefore, developing comprehensive ecological management approaches based on a thorough understanding of wild oat' s basic biology, population ecology, and physiological ecology is essential.

Previous research has focused primarily on wild oat's harmfulness as a farmland weed and the efficacy of chemical control, with limited investigation into the physiological and ecological mechanisms underlying its weed status. Although some studies have analyzed the inhibitory effects of wild oat aboveground parts on wheat seed germination, the impact of underground parts has been largely ignored, hindering a comprehensive understanding of wild oat's allelopathic effects. This study investigated wild oat' s basic biological characteristics, flowering and seed-setting dynamics, seed dispersal patterns, seed germination under stress, seedling growth status, and the allelopathic effects of root systems on wheat, aiming to provide theoretical foundations for developing rational and effective wild oat control measures.

1.1 Experimental Materials

The wild oat population used in this study was naturally distributed in the wheat experimental field of Henan University of Science and Technology. Wild oat seedlings were cultivated from seeds in the laboratory. The test wheat variety was common wheat 'Yujiao 5'.

1.2.1 Basic Biological Characteristics and Flowering/Seeding Dynamics of Wild Oat

During the winter wheat regreening stage and wild oat tillering stage (early March 2014), 20 wild oat plants were randomly selected in the wheat experimental field to measure plant height with a tape measure and investigate tiller numbers. Five 1 m × 1 m quadrats were randomly selected to survey wild oat plant density. Another 20 wild oat plants were randomly selected, tagged, and observed for flowering and seed-setting dynamics at different developmental stages. At the seed maturity stage, 10 wild oat plants were randomly selected, killed at 105 °C for 1 hour, then dried in an oven at 75 °C for 24 hours to determine dry weights of roots, stems, leaves, spikes, and seeds, from which biomass and thousand-grain weight were calculated.

1.2.2 Population Distribution Patterns of Wild Oat and Its Associated Plants

At the late flowering stage of wild oat, a 100 m transect was established from a randomly selected point in the wheat field, with a 1 m × 1 m survey quadrat set every 10 m (10 quadrats total). The number of wild oat plants and main associated weeds in each quadrat was recorded. Population distribution patterns of each species were calculated based on Poisson distribution expectation principles.

1.2.3 Seed Dispersal Characteristics of Wild Oat

When wild oat seeds in the wheat field reached the wax ripeness stage, five 1 m × 1 m quadrats separated by more than 50 m were randomly selected, and all seeds on wild oat plants within the quadrats were marked with fluorescent agent. Centered on these five quadrats, five different distances (0-10 m, 11-20 m, 21-30 m, 31-40 m, and 41-50 m) were established in four different directions. Within each distance interval, five consecutive 1 m × 1 m quadrats were set every 2 m. Fluorescent-marked wild oat seeds were counted at night to determine dispersal distance and density.

1.2.4 Seed Germination Characteristics of Wild Oat

Temperature effects on germination: Three treatments were conducted: room temperature germination, freezing followed by room temperature germination, and constant temperature germination, each with three replicates. Thirty uniformly sized mature wild oat seeds were placed in 120 mm glass petri dishes and germinated under adequate moisture conditions. Room temperature germination was conducted at natural room temperature (10-20 °C) without any temperature treatment. The freezing treatment involved placing seeds in a freezer (−18 °C) for 72 hours before room temperature germination. Constant temperature germination was conducted in a 22 °C incubator. Distilled water was added every 24 hours, and data on bud length, root length, root number, and germination count were recorded.

Salt stress effects on germination: Thirty uniformly sized mature wild oat seeds were placed in 120 mm glass petri dishes, and different concentrations of NaCl solution were added (0 $g \cdot L^{-1}$, 3 $g \cdot L^{-1}$, 6 $g \cdot L^{-1}$, 9 $g \cdot L^{-1}$, 12 $g \cdot L^{-1}$, 15 $g \cdot L^{-1}$, 18 $g \cdot L^{-1}$, 20 $g \cdot L^{-1}$, and 30 $g \cdot L^{-1}$), with 0 $g \cdot L^{-1}$ as the water control. Each treatment had three replicates, and germination was conducted at room temperature for 10 days, with daily recording of germinated seed numbers.

1.2.5 Effects of Salt and Drought Stress on Proline Content and Catalase Activity in Wild Oat Seedlings

Salt stress was simulated using NaCl solutions at concentrations of 0 $g \cdot L^{-1}$, 10 $g \cdot L^{-1}$, 20 $g \cdot L^{-1}$, and 30 $g \cdot L^{-1}$. Drought stress was simulated using PEG 6000 solutions at concentrations of 0 $g \cdot L^{-1}$, 100.0 $g \cdot L^{-1}$, 200.0 $g \cdot L^{-1}$, and 300.0 $g \cdot L^{-1}$ (with solution osmotic potentials equivalent to 0 MPa, −0.5 MPa, −1.0 MPa, and −1.5 MPa, respectively). Thirty uniformly sized mature wild oat seeds were selected, dormancy was broken through low-temperature treatment, and seeds were germinated in 120 mm glass petri dishes with distilled water. After four weeks, when wild oat seedlings had developed 1-2 leaves, 32 petri dishes were randomly divided into two groups of 16 each for salt and drought stress treatments, respectively. Treatment solutions were added sequentially according to concentration gradients, with 10 mL added to each petri dish. After 48 hours of treatment with the first concentration of NaCl or PEG 6000, 0.2 g of wild oat leaf tissue was randomly collected from each petri dish, mixed, and ground to determine proline content and CAT activity. The treatment solution was then poured out, roots were rinsed with distilled water, and the next concentration was added. This process was repeated every 48 hours until proline content and CAT activity were determined for all concentration treatments. The experiment was conducted at room temperature with natural lighting.

1.2.6 Allelopathic Effects of Wild Oat Root Exudates on Wheat Seedlings

Wild oat roots randomly collected from wheat fields were washed clean, crushed, and prepared into concentration gradients of 0 $g \cdot mL^{-1}$, 0.025 $g \cdot mL^{-1}$, 0.050 $g \cdot mL^{-1}$, 0.100 $g \cdot mL^{-1}$, and 0.200 $g \cdot mL^{-1}$ aqueous extracts, with 0 $g \cdot mL^{-1}$ as the water control. Wheat seeds were germinated in 120 mm glass petri dishes under laboratory room temperature conditions. After 7 days, 300 uniformly growing wheat seedlings were selected and transplanted into 200 mm PVC pots containing 0–20 cm topsoil from the wheat field. A total of 15 pots were randomly divided into 5 groups with 3 replicates per group. Different concentration treatments (50 mL) were applied daily for 14 consecutive days. On day 15, wheat seedling height, main root length, aboveground biomass, and root vitality (determined by TTC method) were measured.

All data processing and chart production were completed using Excel 2010 software, and differences between treatments were analyzed for significance using the ANOVA module in SPSS 18.0 statistical software.

2.1 Basic Biological Characteristics and Flowering/Seeding Dynamics of Wild Oat

As shown in Table 1 , mature wild oat plants are tall, with an average height of 76.25 cm and more tillers than wheat. Biomass allocation differs significantly among stems, leaves, and spikes, with the largest proportion allocated to reproductive organs and lower allocation to vegetative organs. Based on grain number per spike, thousand-grain weight, and plant density, wild oat produces more grains per spike than wheat (approximately 35 for wheat). The soil seed bank contains up to 76.8×10^6 seeds per cubic meter.

Plant flowering and seeding dynamics are critical for successful reproduction. Table 2 shows that wild oat began flowering on April 20, reaching peak bloom after 7 days. Seed setting started on May 4, and by May 9, grain filling was essentially complete with kernels beginning to harden, though some plants could still flower (the milky ripeness stage). On May 13, wild oat entered the wax ripeness stage, when about one-third of seeds began natural shedding. By May 21, seeds were essentially fully ripe, with most seeds shed and plants beginning to wither.

2.2 Population Distribution Patterns of Wild Oat and Its Associated Plants

Population distribution patterns result from long-term adaptation and selection of plant biological characteristics to environmental conditions. The population distribution patterns of wild oat and its associated weeds are shown in Table 3 . The main associated plants include *Galium aparine* var. *tenerum*, *Setaria viridis*, and *Alopecurus aequalis*. The V/m values (ratio of variance to mean) for these four major species all exceed 1, indicating that both wild oat and its associated weeds in wheat fields exhibit aggregated distribution patterns, with *Alopecurus aequalis* showing particularly pronounced aggregation.

2.3 Seed Dispersal Characteristics of Wild Oat

Seed dispersal mechanisms significantly influence plant population renewal and community succession. Research on wild oat seed dispersal characteristics (Figure 1 [Figure 1: see original paper]) revealed that seed dispersal density is highest at shorter distances and decreases with increasing distance. The maximum dispersal density occurs within 10 m, reaching 460 seeds $\cdot$ m^{-2}, gradually decreasing with distance and approaching zero at 50 m.

2.4 Seed Germination Characteristics of Wild Oat Under Different Temperature and Salt Stress Conditions

Temperature is a crucial environmental factor affecting seed germination. Wild oat seed germination characteristics under different temperature treatments are shown in Figure 2 [Figure 2: see original paper]. Bud length, root length, and root number increased most significantly under room temperature and freezing-followed-by-room-temperature conditions, being significantly greater than under constant temperature treatment at 7 days ($P<0.01$, Figures 2A, 2B, 2C). The lowest germination rate (approximately 60%) occurred under constant temperature, while room temperature and freezing-followed-by-room-temperature treatments achieved germination rates above 90% with no significant difference between them ($P>0.05$, Figure 2D). These results indicate that variable temperature promotes wild oat seed germination and is beneficial for breaking seed dormancy.

Salt stress is a major abiotic stress during seed germination. The effects of salt stress on wild oat seed germination are shown in Figure 3 [Figure 3: see original paper]. NaCl strongly inhibited germination, with only a few seeds germinating. Over time, except for the 15–18 $g \cdot L^{-1}$ NaCl concentration where virtually no germination occurred (average cumulative germination <2, germination rate <8.3%), other concentrations (3–12 $g \cdot L^{-1}$) showed consistent germination trends, with germination numbers gradually increasing and average cumulative germination between 5-7 (germination rate 16.7%-23.3%). These results demonstrate that wild oat seeds possess certain resistance to NaCl stress, and although germination rates decrease significantly ($P<0.01$), some seeds can still germinate over time.

2.5 Physiological Responses of Wild Oat Seedlings to Salt and Drought Stress

Salt and drought stress are important factors constraining plant seedling growth. The effects of salt and drought stress on proline content in wild oat seedling leaves are shown in Figure 4 [Figure 4: see original paper]. Proline content increased with increasing NaCl concentration (Figure 4A), being significantly greater than the water control ($P<0.01$), though differences between different NaCl concentrations were not significant ($P>0.05$). Proline content also increased with increasing PEG concentration (Figure 4B), with all concentration treatments significantly greater than the control ($P<0.01$). The highest proline content occurred at 200 $g \cdot L^{-1}$ PEG, followed by a slight decreasing trend. Compared with lower PEG concentrations, prolonged high-concentration treatment (300 $g \cdot L^{-1}$) caused a slight but significant decrease in proline content ($P<0.05$).

The effects of salt and drought stress on catalase activity in wild oat seedling leaves are shown in Figure 5 [Figure 5: see original paper]. Under different NaCl concentrations, CAT activity showed fluctuating changes (Figure 5A), following a decrease-increase-decrease pattern with increasing NaCl concentration. The 20 $g \cdot L^{-1}$ and 30 $g \cdot L^{-1}$ NaCl treatments showed significantly greater CAT activity than the 10 $g \cdot L^{-1}$ treatment ($P<0.01$), but all were significantly lower than the water control ($P<0.01$), indicating a stage-specific adaptation process to NaCl stress. Similar fluctuating patterns were observed under different PEG concentrations (Figure 5B), suggesting that wild oat also exhibits stage-specific adaptation to drought stress.

2.6 Allelopathic Effects of Wild Oat Root Exudates on Wheat Seedlings

Allelopathy is common in nature, with some plants influencing others through organic compounds secreted by their roots. The effects of wild oat root aqueous extracts on wheat seedling morphological characteristics and root vitality are shown in Figure 6 [Figure 6: see original paper]. Inhibition of wheat seedling height, root length, biomass, and root vitality increased significantly with increasing extract concentration, reaching highly significant differences compared with the water control at concentrations of 0.100 $g \cdot mL^{-1}$ and 0.200 $g \cdot mL^{-1}$ (Figures 6A, 6B, 6C, 6D). While the effect on wheat dry weight was relatively small, inhibition of root length and seedling height was most pronounced, with root length and root vitality decreasing by 2–4 times compared with the control at the maximum concentration ($0.200\ g \cdot mL^{-1}$) (Figures 6B, 6D). These results demonstrate that wild oat root aqueous extracts have very strong allelopathic effects on wheat seedlings.

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3 Discussion and Conclusion

As a Poaceae family weed, wild oat' s population competitiveness and allelopathic effects are important causes of significant crop yield reduction. Our results demonstrate that strong reproductive capacity is a key aspect of wild oat' s competitive advantage, with a stable and large soil seed bank, consistent with findings by Maxwell and Wu. Aggregated distribution results in high local density, which negatively impacts wheat yield. Additionally, at seed maturity, wild oat biomass is concentrated in stems and spikes (approximately 50% allocation), indicating that wild oat allocates more energy to reproductive organs to ensure reproduction, helping populations survive adverse conditions through seeds. A key characteristic of mature wild oat seeds is extreme dormancy. Physiological and ecological research to identify optimal methods for breaking this dormancy could facilitate concentrated germination followed by immediate control, reducing field seed density. Our results show that wild oat seeds germinate under constant temperature, room temperature, and freezing-followed-by-room-temperature conditions, indicating a wide temperature adaptation range. Shavand et al. demonstrated that wild oat seeds achieve highest germination rates at 2–5 °C, which aligns with our results and confirms that low temperature significantly affects germination and essentially breaks seed dormancy.

Stress resistance is a common plant response to environmental stress. As an important component of the cellular antioxidant system, catalase (CAT) activity is a key indicator of functional damage under stress. In this study, CAT activity in wild oat leaves showed a decreasing-increasing-decreasing trend under salt stress, with significant differences between treatments, indicating that wild oat can adapt to salt stress within a certain range through stage-specific responses. Plant adaptation to salt stress has been demonstrated in numerous studies. Under salt or drought stress, plants accumulate large amounts of free proline to maintain normal cell function, with content increasing as stress intensity increases to help plants adapt to water deficit. Our study shows that proline content increased gradually with salt concentration, indicating that salt stress-induced proline accumulation is an important mechanism for wild oat' s salt adaptation. The absence of significant proline reduction at higher salt concentrations suggests strong salt tolerance. Under drought stress, proline content increased slightly initially but then decreased, likely because as drought intensified and water availability decreased, physiological functions were impaired, leading to significant proline reduction, consistent with findings by Wang Lili et al.

Allelopathic effects of farmland weeds adversely affect the growth and yield of associated crops. Wild oat roots can secrete toxic substances that inhibit the growth and development of other species, providing competitive advantages for establishing stable populations in farmland. Our results show that wild oat root aqueous extracts significantly inhibit wheat seedling height, root length, biomass, and root vitality, with inhibition increasing as extract concentration increases. Similar studies have reported effects of wild oat root extracts on wheat seedling height, root length, and fresh weight, consistent with our findings. However, our study designed concentration gradients to reflect the dose-response relationship of this inhibition. Furthermore, our results demonstrate that wild oat root extracts inhibit wheat seedling root vitality, which directly affects plant physiological function. The allelopathic substances from wild oat roots have been preliminarily identified as scopoletin, coumarin, p-hydroxybenzoic acid, and vanillic acid, though which component plays the dominant role requires further investigation.

In addition to being a malignant farmland weed, wild oat is also a regional invasive plant. The competitive advantages of invasive plants are first manifested in strong reproductive capacity and unique population dispersal mechanisms. Our study shows that wild oat has a plant density of 12.9 plants$\cdot$m^{-2}, allocates more biomass to reproductive organs, exhibits aggregated distribution patterns, and maintains a soil seed bank as high as 76.8×10^6 seeds$\cdot$m^{-3}. These reproductive characteristics ensure population competitiveness and successful invasion. Second, invasive plants possess strong environmental adaptability. Wild oat seeds germinate across a wide temperature range, with maximum germination rates achieved after freezing followed by room temperature treatment, related to their dormancy characteristics. Currently, no particularly effective methods exist to predict wild oat seed germination patterns. Wild oat seedlings demonstrate strong tolerance to salt and drought stress, adapting to varying degrees of harsh environments through proline accumulation and increased CAT activity. Finally, like many other invasive plants, wild oat can secrete allelochemicals from both aboveground and underground parts, exerting allelopathic effects on associated plants. Our results show that wild oat significantly inhibits wheat seedling height, root length, root vitality, and biomass, with inhibition increasing as root extract concentration increases. This allelopathic effect not only restricts normal wheat growth but also helps secure resources and space. Thus, these competitive advantages not only facilitate wild oat’ s successful invasion of farmland but also complicate control efforts.

In summary, investigating wild oat’ s reproductive and stress resistance characteristics and its allelopathic effects on wheat from reproductive and physiological ecological perspectives demonstrates that: (1) Wild oat has strong reproductive capacity, a large soil seed bank, and seed dormancy characteristics; (2) Wild oat exhibits stage-specific adaptation to drought and salt stress, with leaf proline content and CAT activity showing fluctuating decrease-increase-decrease patterns; (3) Wild oat root exudates have allelopathic effects on wheat, primarily manifested as significant inhibition of wheat growth and root vitality.

These characteristics are important reasons why wild oat has become a malignant farmland weed and regional invasive plant. Currently available chemical agents do not provide thorough control and cannot guarantee the safety of associated crops. Therefore, wild oat control should integrate various biological and environmental factors to achieve maximum and more effective management.

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Note: Figure translations are in progress. See original paper for figures.